

## **Diversity and physiology of siderophilic cyanobacteria: implication for the bioenergetics**

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Prior to 2.4 Ga, global oceans were likely significantly enriched in soluble iron (Rouxel, Bekker, Edwards, 2005), a condition that is not conducive to the growth of most contemporary mesophilic cyanobacteria (CB). Recent studies of the mechanisms of iron-deficiency stress in CB suggest that contemporary mesophilic freshwater and marine CB underwent long-term adaptation to a permanent decrease in soluble iron in the ocean environment (Boyer, et al., 1987; Braun, Hantke, and Koster, 1998). Of all extant environments, iron-depositing hot springs may constitute the most appropriate natural models for analysis of the transition of ancestral cyanobacteria (CB) or protocyanobacteria (PCB) (Olson, 2001) from anoxygenic photosynthesis to oxygenic one *and biogeochemical processes in the late Archean and early Paleoproterozoic eras*.

In particular, Olson (2001) proposed the definition for PCB and postulated that the common ancestor of PCB and CB might well have used  $\text{Fe}(\text{OH})^+$  as the principal electron donor for  $\text{CO}_2$  fixation (Widdel, et al., 1993; Ehrenreich and Widdel, 1994; Pierson and Olson, 1989; Olson, 2006). Olson (2001) proposed that the driving force for the evolution of RC2, in addition to RC1, was the necessity to use  $\text{Fe}(\text{OH})^+$  effectively for  $\text{CO}_2$  fixation in the absence of reduced sulfur compounds. The global decrease of dissolved environmental reduced iron could have been the driving force for the transition from anoxygenic to oxygenic photosynthesis (Brown et al., 2007).

Despite the insights into the ecology, evolutionary biology, paleogeobiochemistry, and astrobiology the examination of iron depositing hot springs (IDHS) could potentially provide, very few studies dedicated to the diversity and physiology of cyanobacteria inhabiting IDHS have been conducted. Here we describe the phylogeny, physiology and ultrastructure and biogeochemical activity of several recent CB isolates from two different greater Yellowstone area IDHS, e.g. LaDuke and Chocolate Pots. Phylogenetic analysis of 16S rRNA genes indicated that 6 of 12 new isolates examined could not be placed within established CB genera.

Some of the isolates exhibited pronounced requirements for elevated iron concentrations, with maximum growth rates observed when 0.4–1 mM  $\text{Fe}^{3+}$  was present in the media. However, the pronounced effect of iron limitation on the proliferation of siderophilic CB can be observed only after several passages through iron “free” media. TEM studies of several species of siderophilic CB revealed that the cultures JSC-3 and -11 are probably capable of some sort of pinocytosis of precipitated iron. This phenomenon may explain high tolerance of siderophilic CB to iron deficit. We also found that the stimulation of the growth of siderophilic CB by oxidized iron is accompanied by the decrease of  $\text{O}_2$  evolution by some species after addition  $\text{Fe}^{2+}$  in iron “free” medium.

Siderophilic CB are capable of bioleaching of iron-containing rocks and deposits (Brown et al., 2007). This phenomenon may have adaptive function for CB since the concentration of reduced iron in IDHS has steep negative gradient from a ground water source over a short distance to the bottom edge of a spring where  $\text{Fe}^{3+}$  derivatives are unlimited (Wilson et al., 2000). CB species from this dynamic environment may provide

therefore interesting models for the study  $\text{Fe}^{2+}/\text{Fe}^{3+}$  transport through cytoplasmic membrane as well as for testing Y. Cohen hypothesis that PSI can directly oxidize  $\text{Fe}^{2+}$  (Cohen, 1989).

**Conclusion.** Our results revealed significant variations in the physiological and energetic responses of siderophilic CB to both dissolved and precipitated iron in laboratory settings. Understanding of these variations may provide insights into CB evolution and their interaction with the hydrosphere on early Earth and probably Mars.